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HETEROSTYLY IN SOUTH AFRICAN FLOWERING PLANTS: A CONSPECTUS

ROBERT ORNDUFF

(*Department of Botany, University of California, Berkeley, California*)

ABSTRACT

Heterostyly or related phenomena have been reported in 19 families of flowering plants represented in South Africa. Published studies of this phenomenon are reviewed and it is suggested that the reports of distyly for Capparaceae, Commelinaceae, and Santalaceae are based on misinterpretations of floral structure. Although all native species of *Oxalis* (Oxalidaceae) in South Africa are structurally tristylous, some of these are self-compatible and at least one species is autogamous. Pollen heteromorphism exists in the species of *Oxalis* examined although it does not always follow expected patterns. Most populations of *Oxalis* sampled deviate from equality of representation of the three forms. In some instances this inequality is probably a result of vegetative propagation rather than sexual reproduction. The monomorphic species of *Nivenia* (Iridaceae) are composed of self-compatible long-styled plants that are likely derived from the dimorphic, self-compatible species. The same relationship probably also exists in *Lithospermum* (Boraginaceae). Unusual expressions of distyly are recorded in *Jasminum* (Oleaceae) and *Sebaea* (Gentianaceae). Earlier reports for a number of families are confirmed or amplified. The unique and enigmatic left- and right-handed flowers of various Haemodoraceae and Tecophilaeaceae are described and discussed. Heterostyly is richly represented in the South African flora, but it is evident that little is known about the reproductive systems of any heterostylous South African angiosperm.

UITTREKSEL

HETEROSTILIE BY SUID-AFRIKAANSE BLOMPLANTE

Heterostilie of verwante verskynsels is by 19 families blomplante wat in Suid-Afrika verteenwoordig is, gevind. Gepubliseerde ondersoeke van die verskynsel word in oënskou geneem en dit word aan die hand gedoen dat die verslae oor distilie by Capparaceae, Commelinaceae en Santalaceae op 'n foutiewe vertolking van die blombou berus. Alhoewel alle inheemse *Oxalis* (Oxalidaceae) soorte in Suid-Afrika in bou tristilies is, sommige tog self-vereenigbaar en ten minste een soort autogaam is. Stuifmeel heteromorfisme bestaan in die soorte van *Oxalis* wat ondersoek is, alhoewel dit nie altyd die verwagte patrone volg nie. Meeste *Oxalis* bevolkings getoets wyk af van die gelykheid van voorstelling van die drie vorms. In sommige gevalle is die verskille moontlik 'n gevolg van vegetatiewe voortplanting meer as geslagtelike voortplanting. Die monomorfiese *Nivenia* (Iridaceae) soorte word saamgestel uit self-vereenigbare lang styl plante wat moontlik ontwikkel het uit dimorfiese, self-vereenigbare soorte. Dieselfde verwantskap bestaan moontlik by *Lithospermum* (Boraginaceae). Ongewone voorkoms van distilie word aangeteken vir *Jasminum* (Oleaceae) en *Sebaea* (Gentianaceae). Vroëre verslae oor 'n aantal families word bevestig en aangevul. Die besondere en enige links-en-regs-draaiende blomme van verskeie Haemodoraceae en Tecophilaeaceae word beskryf en bespreek. Heterostilie kom volop in die Suid-Afrikaanse flora voor maar dit is duidelik dat baie min oor die voortplantingsisteme van enige heterostilie angiosperme bekend is.

INTRODUCTION

Heterostyly has been reported in approximately 24 families of flowering plants of diverse phyletic positions (Vuilleumier, 1967). The term refers to

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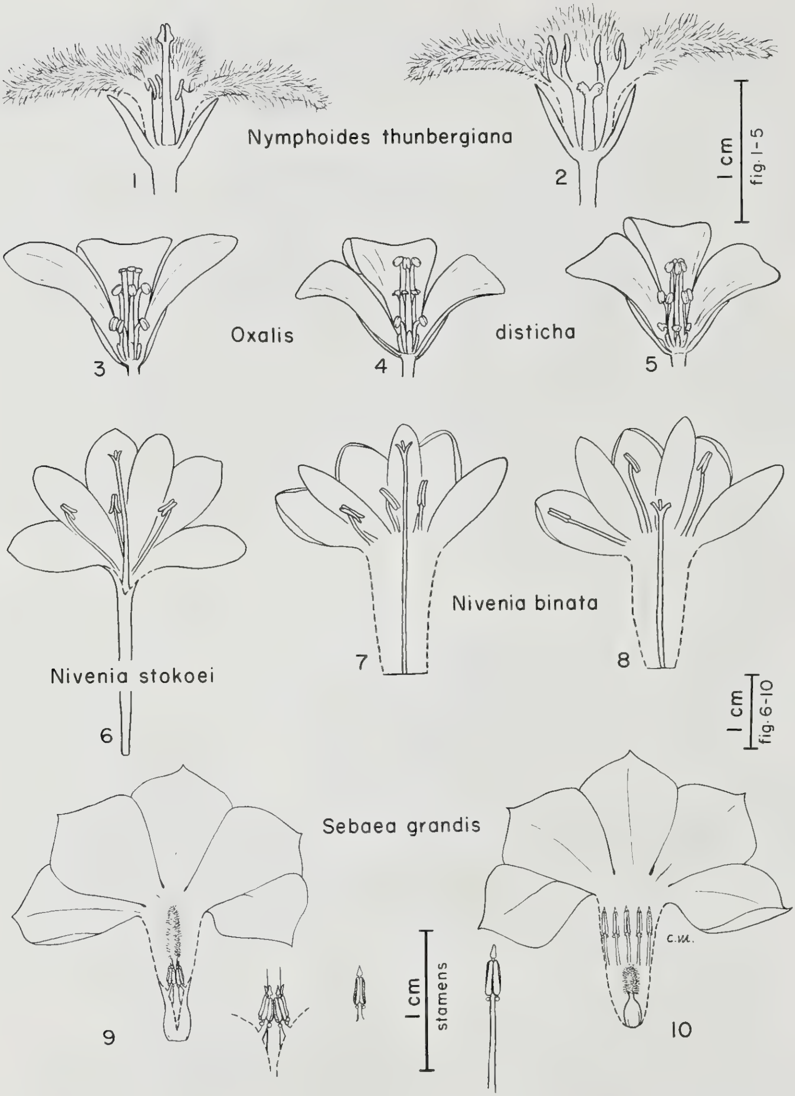

Nymphoides thunbergiana
1
2
1 cm
fig. 1-5
Oxalis
disticha
3
4
5
Nivenia stokoei
6
7
Nivenia binata
8
1 cm
fig. 6-10
Sebaea grandis
9
1 cm
stamens
10
c.m.

dimorphism or trimorphism in floral features that includes differences in length of styles; position of stamens; size of stigmas and stigmatic papillae; size, sculpturing, colour, and contents of pollen grains; physiological reaction of pollen and carpellary tissue; and an array of other morphological and physiological features of flowers. In the expression termed distyly, some plants of a species bear flowers with long styles and short stamens; others have flowers with short styles and long stamens (e.g., Fig. 1, 2). This floral dimorphism is generally accompanied by a variable number of the other differences between the two floral forms that are listed above. In tristyly, three types of plants occur: those having long-styled flowers with two sets of anthers below the level of the stigma; those having mid-styled flowers with one set of anthers borne above the stigma and a second set below; and those having short-styled flowers with two sets of anthers above the stigma (e.g., Fig. 3–5). As in distyly, there are generally other morphological features that distinguish the flowers of each of the three forms of a tristylous species. Tristyly is rare and occurs only in Lythraceae, Pontederiaceae, and Oxalidaceae.

Although heterostyly has been known as a morphological feature of various flowering plants for several centuries, it was not until the middle of the 19th century that Darwin in Britain and Hildebrand in Germany began to understand the biological significance of this floral heteromorphism. Contemporaneously, both men demonstrated that heterostyly is generally associated with an incompatibility system which allows only certain fertilizations to take place. These workers believed that the positional relationships of anthers and stigmas enhance pollen transfer between anthers and stigmas at equivalent positions. Thus, heterostyly came to be viewed as a morphological-physiological mechanism that promotes outcrossing, though in fact there are still only a few empirical observations of field populations which explore this supposition.

Heterostyly has been reported or suggested to occur in a number of genera belonging to nearly twenty families of flowering plants represented in South Africa. With a few exceptions, the floral morphology and reproductive systems of these taxa have not been investigated. During eight months in 1970 and 1971 I studied a number of these plants in the field and subsequently in cultivation, examined herbarium specimens in South Africa and Britain, and conducted a survey of the relevant literature. The purpose of this paper is to

FIG. 1–10.

Heterostyly in representative South African plants.

Fig. 1–2, Long- and short-styled flowers of *Nymphoides thunbergiana* (*Tim s.n.*). Fig. 3–5, Long-, mid-, and short-styled flowers of *Oxalis disticha* (*Ornduff 7297*). Fig. 6, Flower of the monomorphic *Nivenia stokoei* (*Goldblatt s.n.*). Fig. 7–8, Long- and short-styled flowers of *Nivenia binata* (*Ornduff 7570*). Fig. 9–10, Long- and short-styled flowers of *Sebaea grandis* (*Hilliard & Burtt, s.n.*) with details of the stamens of each form.

summarize what is known of heterostyly in South African plants based on studies published by others, to present a number of original observations, and to suggest areas for future research in this interesting phenomenon which is so richly developed in the flora of the Republic.

BORAGINACEAE

There are reports of distyly for a South American species of *Cordia* (Darwin, 1877) but material of the South African species in the Compton Herbarium was inadequate for verification of this trait. My observations on the introduced South American annual weed *Amsinckia hispida* (Ruiz & Pavon) Jtn. indicate that it is homostylous and self-pollinating, although some of the North American species in this genus are distylous (Ray and Chisaki, 1957). The four species of *Lithospermum* in South Africa are monomorphic (Johnston, 1952) though apparently not homostylous, thus paralleling in some respects the condition noted below for *Nivenia* (Iridaceae). Although distyly is known to occur in *Anchusa*, I have been unable to find a report for the South African species.

CAESALPINACEAE

Vogel (1955) has stated that *Bauhinia esculenta* Benth. (= *B. burkeana* Burch.) is distylous in South Africa, although neither Urban (1883) nor subsequent workers have remarked on this trait. Vogel indicates that both the long-styled and the short-styled form produce seed, thus ruling out the possibility of dioecism. However, the pollen is said to be monomorphic, although no measurements are given (Vogel, 1955). The occurrence of distyly in *Bauhinia* is a unique occurrence of this trait in the legumes sensu lato (Vuilleumier, 1967) and a fuller documentation of the morphological expression of distyly and the associated breeding systems of the South African species of this genus is warranted. Vogel also states that the related *B. fassoglensis* Kotschy is monomorphic, though the flowers of the population he visited were all long-styled. However, on the basis of a floral description given by Urban, short-styled plants of this species may also exist. As in *Nivenia*, the occurrence of monomorphic but not homostylous populations of *B. fassoglensis* suggests that in *Bauhinia* heterostyly is not accompanied by self-incompatibility.

CAPPARACEAE

Vogel (1955) reported distyly and dioecy in the widespread *Cleome angustifolia* Forssk. (as *C. diandra* Burch.). Heterostyly is otherwise unknown in the family (Vuilleumier, 1967). Codd and Kers (1970) point out that perfect, male-sterile, and female-sterile flowers may occur intermittently along the racemes of this species and that "some specimens have flowers which approach female sterility by having normal stamens but much impoverished pistils". It is this condition which these workers believe misled Vogel into considering the species to be heterostylous. Thus the Capparaceae can probably be removed from the list of families in which heterostyly occurs.

COMMELINACEAE

Vogel (1955) states that *Aneilema aequinoctiale* (Beauv.) Knuth is distylous although Morton (1966) makes no mention of this trait. Vogel's brief discussion of this species does not make it clear whether it is distylous or merely androdioecious. Van Druten (1959) mentions that "a large number of the flowers are sterile, having an undeveloped ovary and short or absent style". In view of the uncertainties concerning the floral morphology of *A. aequinoctiale* and the very brief attention devoted to this species by Vogel, it clearly merits additional investigation. It seems doubtful if the species is heterostylous.

CONNARACEAE

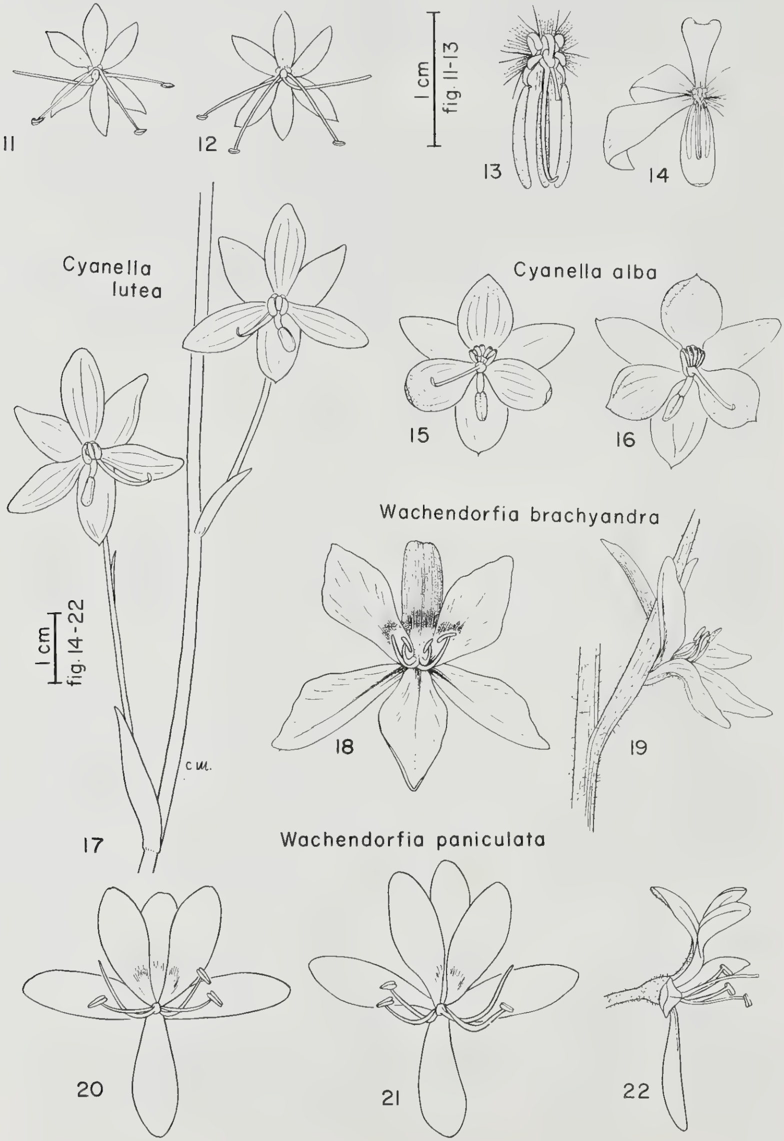
Cnestis natalensis (Hochst. ex Krauss) Planch. & Sond. is distylous (Mendes, 1966) but there are no reports concerning its breeding system.

ERYTHROXYLACEAE

Distyly and dioecism are widespread in the genus *Erythryoxylum* (cf. Vuilleumier, 1967). Robson (1963) reported that *E. emarginatum* Thonn. and *E. delagoense* Schinz are dimorphic. My observations on herbarium specimens of *E. brownianum* Burtt-Davy indicate that this species is also distylous.

GENTIANACEAE

Distyly has been reported for the African genus *Sebaea* (= *Exochaenium* = *Belmontia*; Gilg, 1895). The peculiar distyly of the southern African *S. grandis* (E. Mey.) Steudel was illustrated by Hill (1908) and further elaborated by Vogel (1955). In this species, the stigmatic papillae of the short-styled form are larger than those of the long-styled form, a condition contrary to that usually encountered in distylous species. Measurements of 20 pollen grains each from 2 long- and 2 short-styled plants of this species collected in the eastern Transvaal by Mrs. L. E. Davidson indicate an average pollen size of 15,4 μ for long-styled flowers and 16,7 μ for short-styled flowers, a difference that is significant on the basis of a *t*-test. Hill (1908) also mentions that the anthers of long-styled flowers are concrescent and extrorse, whereas in the short-styled flowers they are free and introrse. Pole Evans (1929) further states that the stamens in long-styled flowers have almost sessile anthers, while anthers of short-styled flowers have filaments. My own studies confirm these observations (Fig. 9, 10). Goldblatt (pers. comm.) reported that in the small population he


Barberetta aurea
11
12
1 cm
fig. 11-13
13
14
Cyanella lutea
Cyanella alba
15
16
1 cm
fig. 14-22
Wachendorfia brachyandra
18
19
c.m.
17
Wachendorfia paniculata
20
21
22

sampled in the Transvaal highlands there were 15 long- and 9 short-styled plants present.

Marais and Verdoorn (1963) also describe "medium" styled flowers; this, plus the description of *Exochaenium grande* var. *homostylum* Hill (1908), suggests the possibility that some sort of homostyly also occurs in this species, although, as pointed out by Marloth (1909) for *Sebaea exacoides* (L.) Schinz, the style of that species lengthens during the flowering process. Marloth further remarked that each flower of this species possesses "two distinct stigmatic organs, viz. a bilobed normal stigma and a lower one about the middle of the style. It has not yet been decided whether both kinds are always functionally perfect, for they may represent a veiled state of heteromorphism, viz. in some individuals of a species the upper stigma and in others the lower one may be receptive . . ." Clearly, *Sebaea grandis* and its congeners merit further study.

HAEMODORACEAE

Wilson (1887) reported a curious condition in *Wachendorfia*, in which the style of the flowers of some plants is deflected to the left and in others to the right. This is accompanied by differences in the position of the 3 stamens of the flower; in flowers with "left-handed" styles the third stamen is deflected along with the style and the remaining two stamens are deflected to the right. A reverse situation exists in "right-handed" flowers (Fig. 20–22). Wilson suggested that this condition represents a mechanism associated with promoting cross-pollination between the two forms. His sparse data suggest that the plants he worked with are moderately self-incompatible and that the highest seed set was obtained when crosses were made between the two floral forms.

Field studies of the 5 currently recognized species of *Wachendorfia* (Barker, 1950) indicate that all of them are dimorphic. In the large-flowered *W. paniculata* Burm. in which the perianth segments are spreading, ratios of "left" and "right" in natural populations are 1:1 (Table 1), suggesting that these large-flowered species are largely outcrossed. However, in the small-flowered *W. brachyandra* Barker, the short stamens and style are somewhat erect with the anthers and stigma in close proximity (Fig. 18, 19). This observation, plus the fact that populations of this species deviate from a 1:1 ratio (Table 1) suggest that

FIG. 11–22.

Floral morphology of representative South African Haemodoraceae and Tecophilaeaceae.

Fig.11–12, "Left-" and "right-handed" flowers of *Barberetta aurea* (*Hilliard & Burtt 3476*). Fig. 13–14, Details of stamens, styles, and flower of *Cyanella orchidiformis* (*Ornduff 7187*). Fig. 15–16, "Left-" and "right-handed" flowers of *Cyanella alba* (*Ornduff 7424*). Fig. 17, Portion of inflorescence of *Cyanella lutea* (*Ornduff 7355*) showing "left-" and "right-handed" flowers. Fig. 18–19, "Left-handed" flower of *Wachendorfia brachyandra* (*Ornduff 7542*). Fig. 20–22, "Left-" and "right-handed" flowers of *Wachendorfia paniculata* (*Ornduff 7162*) with lateral view of latter.

TABLE 1.

Numbers of plants with "left-handed" and "right-handed" flowers in populations *Wachendorfia*. Equality decision based on the Z test.

Locality (Cape Prov.)	Left-handed	Right-handed	1:1
(W. paniculata Burm.):			
RO 7308; Mamre	44	47	yes
RO 7328; Bokbaai	44	40	yes
RO 7343; Between Goudini and Breërivier	27	34	yes
RO 7354; Worcester	55	60	yes
(W. brachyandra Barker):			
RO 7542; Kirstenbosch	49	11	no

W. brachyandra carries on some degree of autogamy. Studies of the pollen indicate that there is no consistent size heteromorphism associated with the floral dimorphism in the genus.

A rare relative of *Wachendorfia* is *Barberetta aurea* Harv., which is known from only a few localities in the Transkei and Natal. My observations of *Barberetta* in the field indicate that its floral dimorphism is similar to that of *Wachendorfia*, though some populations seemingly are monomorphic through vegetative propagation from an initial colonizer. The deflection of the style of *Barberetta* was noted by Geerinck (1971) although he apparently failed to realize that the species is dimorphic in the direction of this deflection (Fig. 11, 12). Whether or not this floral dimorphism is associated with an outbreeding system is unknown.

Another genus in the Haemodoraceae is the small genus *Dilatris*, which consists of 5 species restricted to the southwestern Cape Province, South Africa (Barker, 1940). Despite certain morphological differences between *Dilatris* and *Wachendorfia*, recent systematists consider that these two genera are rather closely related (de Vos, 1956). It is interesting to note that although the styles of *Dilatris* flowers are deflected in a fashion similar to those of *Wachendorfia*, both "left-" and "right-handed" flowers occur in the same inflorescence. Field studies of *D. corymbosa* Berg. indicate that approximately equal numbers of "left-" and "right-handed" flowers are open on a single plant at one time. The relationship of this condition to a breeding system is perplexing and merits further study.

Cyanella has sometimes been included in the Haemodoraceae (Barker, 1950) as well as other monocot families, but recent evidence suggests that the genus is a member of the Tecophilaeaceae (Hutchinson, 1944: de Vos, 1961; Geerinck, 1969). Despite its seemingly distant relationship to the Haemodoraceae, some species of *Cyanella*, such as *C. alba* L. f. and *C. lutea* L. f., show the same floral structure as *Dilatris* with respect to style and stamen deflection in the flowers of one plant (Fig. 15–17). However, other species of *Cyanella*, such as *C. capensis* L. and *C. orchidiformis* Jacq. have straight styles and stamens (Fig. 13, 14). It is difficult to believe that the similarities between the floral structure of *Cyanella* and *Dilatris* are a result of parallel evolution; they suggest that these genera are more closely related than their placement in separate families would indicate.

In *Cyanella* and *Dilatris* of the Haemodoraceae (see above) it is difficult to see the adaptive value of "left-handed" and "right-handed" flowers in the same inflorescence. For field biologists interested in reproductive biology, both genera present intriguing and as yet unsolved problems.

IRIDACEAE

Distyly has been reported for two South African genera of Iridaceae. Adamson (1931) reported distyly for two species of *Nivenia*. Later, Brown (1933), Lewis (1934), and Weimarck (1940) observed the trait in various species of this relict woody genus of the southwestern Cape Province. At least three species—*N. dispar* N. E. Brown, *N. corymbosa* (Ker) Baker, and *N. binata* Klatt are definitely distylous (Fig. 7, 8). Mulcahy (1965) reported dimorphism in pollen size and wall patterns for the latter species. Other species, such as *N. capitata* (Klatt) H. Weimarck, *N. stokoei* (Guthrie) N. E. Brown, and *N. levynsiae* H. Weimarck are monomorphic (Fig. 6). The condition of still other species is uncertain; herbarium specimens are inadequate for a comprehensive confirmation of floral morphology and the literature for these is unclear on the point.

There is some indication that the heterostyly of *Nivenia* is different in some important respects from that which occurs in other plant families. A population sample of 54 plants of *N. binata* (Ornduff 7570, Swartberg Pass) indicated that long-styled plants outnumber short-styled ones in a ratio exceeding 2:1, suggesting either that the genetic basis of distyly in this species is not of the simple diallelic type that occurs in other families; or that the species is not self-incompatible and is incompletely outcrossing; or that the short-styled form has a lower viability than the long-styled form. The monomorphic species of *Nivenia* that I have investigated are not homostylous, but resemble the long-styled form of distylous species (Fig. 6). This observation led to the hypothesis that the dimorphic species are self-compatible, a conclusion consistent with the second explanation for the aberrant population composition noted above in the dimorphic species, and that monomorphism has developed by loss of the *S* (short-styled) allele from the dimorphic species rather than by the development of homostyly. This assumes that the genetic basis of distyly in *Nivenia* is the usual diallelic, single locus system in which *ss* is the genotype of the long-styled form and *Ss* is the genotype of the short-styled form. Selfing of a single long-styled plant of *N. corymbosa* (Ornduff 7666, Bains Kloof) indicated this plant to be self-compatible; likewise, the high seed production of isolated plants of the fully monomorphic *N. stokoei* indicates that this species, too, is self-compatible. The occurrence of self-compatible monomorphism without homostyly in species of a genus in which distyly also occurs is perhaps unique among the 24-odd angiosperm families in which heterostyly is known to occur. Clearly, *Nivenia* deserves further experimental investigation.

A second genus of Iridaceae in which heterostyly has been reported is *Geissorhiza* (Bolus, 1930; Lewis, 1954). Bolus' description of the flowers of *G. heterostyla* L. Bolus suggests that it is trimorphic. My observations of a population cultivated at Kirstenbosch (originally from the Nieuwoudtville area) indicate that the species is dimorphic with respect to style length, though the position and length of the stamens are variable. In a sample of 30 plants from this population the length of style fell into two classes. One class consisted of 16 plants with styles 5,5 mm long or longer ($\bar{x} = 8{,}4$; range: 5,5–9,0) and a second class consisted of 14 plants with styles under 5,5 mm long ($\bar{x} = 3{,}8$; range: 2,5–5,0). The majority of flowers in the latter category had styles less than 4,0 mm long.

In its floral morphology, *Geissorhiza heterostyla* is reminiscent of various *Narcissus* species (Fernandes, 1964–65; Dulberger, 1964), though in these species the style-length differences are unassociated with incompatibility groupings. The possible relationship of the stylar dimorphism of *G. heterostyla* to an outbreeding system has yet to be elucidated.

The unusual expression of heterostyly in *Nivenia* and *Geissorhiza* merits further investigation, ranging from a documentation of the characters associated with heterostyly in these genera to an investigation of the presence and nature of an associated incompatibility system.

Linaceae

Although distyly is widespread in the genus *Linum*, the South African species are apparently all homostylous (Alefeld, 1863; Winkler, 1931).

Lythraceae

Of particular interest in South Africa is the genus *Nesaea*, which reportedly has dimorphic, trimorphic, and homostylous species in sections Hemiastrum and Salicariastrum (Koehne, 1903). For example, in section Salicariastrum, *N. schinzii* Koehne and *N. sagittifolia* (Sond.) Koehne are trimorphic, *N. woodii* Koehne is dimorphic, and such species as *N. kuntzei* Koehne and *N. rivularis* (Wood & Evans) Koehne are homomorphic. It is not clear whether all the homomorphic members of these sections are homostylous or whether their flowers are "morphologically heterostylous" and only one (presumably self-compatible) form persists. The evolutionary relationships between the heterostylous condition and the homomorphic condition (as well as the nature of the latter) would be very interesting to work out, especially in view of the similar relationships in floral morphology that exist among the species of the related genus *Lythrum* (Darwin, 1877; Ornduff, unpub.) and in *Oxalis* section Corniculatae (Eiten, 1959, 1963; Ornduff, 1972). Field studies combined with a subsequent crossing program and study of the floral morphology of the southern African *Nesaea* species should provide some interesting insights into the comparative evolution of reproductive systems in this genus.

MENYANTHACEAE

The distyly of *Villarsia capensis* (Houtt.) Merrill and *Nymphoides thunbergiana* (Griseb.) O. Kuntze in South Africa has been noted by Marloth (1932a) and Marais and Verdoorn (1963). Self-pollinations of both species indicate that they are strongly self-incompatible. In Australia, where 12 species of *Villarsia* occur, only *V. exaltata* (Sol.) G. Don is distylous; the other species are homostylous (Aston, 1969) though not necessarily self-compatible (Ornduff, unpub.).

OLEACEAE

The two species of *Schrebera* in South Africa are heterostylous (Verdoorn, 1956; 1963). Verdoorn (1963) has also described distyly in South African species of *Jasminum*, although she states that the flowers are "usually" heterostylous. Her descriptions of the flowers of *J. multipartitum* Hochst. and *J. quinatum* Schinz indicate that these species definitely are distylous, but suggest the possibility that some other species might be monomorphic. Medley-Wood (1898) indicated that *J. streptopus* E. Mey. is dimorphic. My own observations of various South African species of the genus confirm Verdoorn's observations on two species and further indicate that *J. angulare* Vahl, *J. fluminense* Vell., *J. breviflorum* Harv., and *J. glaucum* (L.f.) Ait. are distylous. However, in some specimens of *J. fluminense* the stigma that terminates a very long style is only slightly exserted beyond the anthers, which are situated at the mouth of the corolla tube. In normal long-styled flowers the anthers are situated within the tube. It seems probable that the aberrant flowers represent plants that are long-homostylous, since plants with normal long-styled flowers also occur in this species.

OXALIDACEAE

Approximately half the world's species of *Oxalis* are endemic to South Africa and most of these are localized in the Cape Province. Jacquin (1794) was probably the first botanist to describe heterostyly in South African species of *Oxalis*, but he mistakenly interpreted the floral trimorphism to represent specific differences. Thus, *O. macrogyna* Jacq., *O. fallax* Jacq., and *O. luteola* Jacq. refer to the long-, mid-, and short-styled forms of *O. luteola*. Later, Hildebrand (1867) reported heterostyly in several South African species and pointed out Jacquin's error. Salter (1944) stated that all the species native to South Africa are "probably" tristylous, though in some very rare species not all stylar forms have been observed. Likewise, Marloth (1925) stated unequivocally that "all indigenous species are trimorphic". My own investigations of several dozen species in the field, garden, and herbarium suggest that it is probably true that all South African species of the genus are morphologically tristylous (Fig. 3–5), but that this morphological heteromorphism is not always associated with outcrossing or with self-incompatibility.

Darwin (1877) reported that the short-styled form of *O. compressa* L.f. (section Cernuae) and of *O.* "*Bowii*" (the identity of which he questioned; = *O. bowiei* Lindl., section Cernuae?) produced no seed. The three forms of *O.* "*speciosa*" (= *O. purpurea* L., section Stictophyllae?) produced some seed by self- and other illegitimate pollinations, though seed production was lower than that of legitimate crosses, indicating that this species has a residual self-incompatibility. Hildebrand (fide Darwin, 1877) has suggested that the trimorphic *O. incarnata* L. (sect. Oppositae) produces cleistogamous flowers. I have not confirmed this in the populations that I have examined in the field and in cultivation. Salter (1944) reported that a mid-styled clone of *O. flava* L. (sect. Crassulae) grown at Kirstenbosch produced no seed, and that the short-styled form of *O. caprina* L. (sect. Cernuae), introduced and weedy on the Cape Peninsula, also produces no seed in the absence of other floral forms of the species. Likewise, Salter noted that isolated monomorphic populations of *O. pes-caprae* L. (sect. Cernuae) do not produce seed. In contrast, my studies indicate that the small-flowered *O. pusilla* Jacq. (sect. Angustatae), though structurally trimorphic, sets abundant seed through apparent spontaneous self-pollination. Results of artificially selfing the three floral forms of the closely related large-flowered *O. glabra* Thunb. (sect. Angustatae) indicate that this species is apparently self-incompatible.

Selfing of the three forms of *Oxalis disticha* Jacq. (Fig. 3–5), *O. dines* Ornduff, *O. uliginosa* Schlecht. (all sect. Campanulatae), and *O. massoniana* Salter (sect. Angustatae) produced no seed, indicating that these species are strongly self-incompatible. Selfing of long-styled plants of *O. obtusa* Jacq. (sect. Oppositae) and *O. purpurea* L., and of short-styled plants of *O. dregei* Sond. (sect. Campanulatae) produced no seed, suggesting that these species likewise are self-incompatible. Long-styled plants of *O. versicolor* L. (sect. Angustatae) produced some seed upon selfing. Thus, at least within the large section Angustatae, autogamy, self-compatibility, and self-incompatibility exist, though all species have heteromorphic flowers.

It seems probable that homostyly has not evolved in South African species of *Oxalis* as it has, for example, in the North American section Corniculatae (Ornduff, 1972) and in section Ionoxalis (Denton, 1973). Nevertheless, in some species "effective homostyly" has been achieved by reduction in total floral size and the development of some mechanism which insures selfing (as in *O. pusilla*), though the mechanics of this remains to be demonstrated.

Hildebrand (1867) reported pollen size heteromorphism in the few South African *Oxalis* species available to him. My studies of 5 species belonging to 3 sections indicate pollen size heteromorphism is present in all of these species (Table 2). In general, pollen from the longest set of anthers is larger than that from the mid-level anthers, and pollen from the latter set of anthers is larger than that from the short-level anthers. A few exceptions exist, as for example in *O. dines* and *O. massoniana* where the pollen of mid- and long-level anthers is the same size. Furthermore, in some species there is not a good correspondence in pollen size from anthers at equivalent levels in two forms. For example, the pollen from long-level anthers of Mid and Short forms and from mid-level anthers of Long and Short forms does not correspond in size in *O. monophylla* L. and *O. massoniana*. The significance of these descrepancies is unknown and may merely represent an artifact of sampling. However, they may also suggest breeding systems that deviate from that expected in "normal" trimorphic species (cf. data for sect. Corniculatae, Ornduff, 1972).

TABLE 2.

Pollen size in South African *Oxalis* species, based on sample sizes of 20 pollen grains each. Average measurement and range (in parentheses) are given in microns.

Species and Locality (Cape Prov.)	Floral form	Long	Mid	Short
(Campanulatae):				
O. disticha 7297; Near Koperfontein	Long	—	44,4 (42,9–46,8)	37,7 (35,1–40,0)
	Mid	58,3 (50,7–62,4)	—	37,3 (35,1–41,0)
	Short	54,2 (53,0–57,5)	44,8 (42,9–46,8)	—
O. dines 7471; Botterkloofpas	Long	—	40,5 (35,1–42,9)	36,6 (33,2–39,0)
	Mid	49,3 (44,9–52,6)	—	38,0 (35,1–41,0)
	Short	48,8 (44,8–54,6)	48,2 (44,8–50,7)	—
O. uliginosa 7209; Near Kamieskroon	Long	—	48,3 (41,0–52,6)	44,5 (39,0–48,8)
	Mid	57,8 (54,6–60,4)	—	39,0 (35,1–41,0)
	Short	56,8 (48,8–60,4)	47,3 (42,9–58,5)	—
(Angustatae):				
O. massoniana 7453; Near Nieuwoudtville	Long	—	38,3 (37,0–42,9)	32,5 (29,2–35,1)
	Mid	48,6 (44,8–54,6)	—	36,2 (33,2–39,0)
	Short	43,0 (39,0–46,8)	44,1 (37,0–52,6)	—
(Incertae Sedis):				
O. monophylla 7140; Lions Head, Cape Town	Long	—	44,2 (41,0–48,8)	35,8 (31,2–39,0)
	Mid	51,6 (39,0–56,6)	—	33,4 (29,2–35,1)
	Short	38,9 (37,0–44,8)	34,4 (33,2–39,0)	—

Eighteen population samples of six *Oxalis* species were taken in the field in South Africa and the representation of the various stylar forms was determined in these populations (Table 3). Particular emphasis was placed on *O. pes-*

TABLE 3

Representation of floral forms in South African species of *Oxalis*. Equality decision is based on the Z test.

Species	Locality (Cape Prov.)	Long	Mid	Short	Equality
(Sect. Angustatae):					
O. glabra 7040	Disturbed roadside nr. Durbanville .	21	1	2	no
(Sect. Oppositae):					
O. incarnata 7271	Disturbed roadside, Kirstenbosch. .	30	0	0	no
,, 7278	Oak woodland, Kirstenbosch . . .	159	46	20	no
O. obtusa 7037	Between Stellenbosch and Paarl . .	21	32	22	yes
,, 7118	Steenbergs Cove	64	53	43	yes
O. luteola 7039	Between Klapmuts and Durbanville .	11	8	10	yes
,, 7087	Kenilworth race course, Cape Town .	40	40	21	no
,, 7106	N. of Olifantsbos	27	23	33	yes
(Sect. Stictophyllae):					
O. purpurea 7273	Weedy, Kirstenbosch	14	60	25	no
,, 7276	Non-weedy, Kirstenbosch	39	52	54	yes
(Sect. Cernuae):					
O. compressa 7286	Kalbaskraal	82	59	82	no
,, 7293	Between Malmesbury and Hopefield .	56	51	41	yes
O. pes caprae 7038	Weedy, Klapmuts	12	38	31	no
,, 7041	Weedy, Stellenbosch	7	3	39	no
,, 7272	Weedy, Kirstenbosch	53	164	8	no
,, 7301	Non-weedy, between Hopefield and Langebaan	87	56	88	no
,, 7296	Non-weedy?, between Hopefield and Malmesbury	70	60	57	yes
,, 7292	Non-weedy?, between Hopefield and Malmesbury	59	49	56	yes
Sect. Campanulatae):					
O. disticha 7297	Near Koperfontein	46	49	41	yes

caprae, a species that has a very wide distribution in South Africa. Outside South Africa, this species is a widely distributed and notorious introduced pest of arable lands in Australia, California, Britain, and the Mediterranean area (see Symon, 1961; Lower, 1963; Galil, 1967, 1968). Lower (1963) has suggested that the weedy strain of *O. pes-caprae* "is a sport, either artificial or natural, of the 'maritime' ecotype which has developed elsewhere". Over most of its range as a weed, *O. pes-caprae* appears to be a sterile pentaploid (Yamashita, 1935; van der Pijl, 1968), though Symon (1961) indicates that seed is formed (presumably by fertile tetraploids) in some areas of South Australia where the species has been introduced. My own field observations indicate that in the relatively restricted area of the southwestern Cape Province, *O. pes-caprae* is both a well behaved native and a vineyard weed. In two of the three non-weedy populations examined, long-styled, mid-styled, and short-styled plants are present in equal numbers, but in the weedy populations these forms are unequally represented although such weedy plants are sexual (Table 3). In two of these weedy populations, mid-styled plants predominate. Similarly, a weedy population of *O. purpurea* deviates from equality of representation, with Mids predominating, although in a non-weedy population of this species the three forms are present in a 1:1:1 ratio. Salter (1944) stated that "the short-styled form [of *O. incarnata*] appears to be very rare, if existent at all". In one population of *O. incarnata*, Longs only were present, but in another population the three floral forms were present, although Longs predominated. Overall, 10 of the 18 populations of various *Oxalis* species sampled deviate from equality.

There are at least two complementary explanations that can be offered to account for inequality of representation of the 3 floral forms in *Oxalis*. All indigenous South African *Oxalis* species are bulbous and probably most of these can reproduce asexually by means of increase in number of bulbs (Salter, 1944). My field observations of several species suggest that sexual reproduction by seeds is a rare event, and that much of the increase in population size is due to vegetative propagation. It is probable that sexual reproduction occurs largely after an ecological disturbance such as fire or clearing. Under these circumstances, severe reduction of size of the parental populations due to these ecological disturbances may result in inequality of genotypes due to chance, and one consequence of this is inequality of representation of the three forms in the succeeding, sexually produced generation as a result of this initial unbalance of founder genotypes. To this is added the possibility that some populations of *Oxalis* species may be established initially by the chance dispersal to a new site of one or few bulbils; this, followed by subsequent asexual reproduction, would also result in deviations from a 1:1:1 ratio of the three floral forms. In species that are weedy, such as *O. pes-caprae*, vegetative spread of one or a few genotypes in a population may be much enhanced by cultivation of the soil, and in a number of Cape vineyards that I visited, plants occurring for several metres along the rows of grape vines were of a single form, further confirming the suggestion that the propagation of such weeds is enhanced by cultivation.

PLUMBAGINACEAE

Distyly was reported for *Plumbago auriculata* Lam. (as *P. capensis* Thunb.) by Dahlgren (1918) and by Marloth (1932b) but not mentioned for any species in the genus by Dyer (1963). Baker (1953) reports that five species of *Limonium* sect. Limonium in the Cape are dimorphic but that the four species of the exclusively South African section Circinaria are monomorphic. Dahlgren (1970) has reported distyly in *Dyerophytum indicum* (Gibs ex Wight) O. Kuntze but Dyer (1963) makes no mention of this trait for *D. africanum* (Lam.) O. Kuntze.

PONTEDERIACEAE

Tristyly has been reported for some species of *Heteranthera*, but Marloth (1915) reports that cleistogamy occurs in the South African *H. kotschyana*

Fenzl, indicating that this species is probably monomorphic. Although *Eichhornia crassipes* is not native to Africa, it is a troublesome weed in parts of the Republic and in South West Africa. Wild (1961) reports erroneously that the styles of this species are "sometimes of three different lengths in the same plant". There have been repeated reports of tristyly for this species, but there is no evidence that the short-styled form exists (see Ornduff, 1966), and in any case only a single type of flower is borne by each individual plant.

RUBIACEAE

The largest number of heterostylous genera of any angiosperm family occurs in Rubiaceae (Vuilleumier, 1967). In South Africa, species such as *Oldenlandia rupicola* (Sond.) O. Ktze., *O. muscosa* Brem., and *O. affinis* (R. & S.) DC. are distylous, whereas others, such as *O. corymbosa* L., *O. capensis* L.f., and *O. caespitosa* Hiern. are homostylous (Bremekamp, 1952; Bir Bahadur, 1968). In some species, such as *O. rosulata* K. Sch. and *O. herbacea* (L.) Roxb. there are heterostylous varieties and other, homostylous ones.

Pentodon pentander (Schum.) Vatke, *Agathisanthemum bojeri* Klotzch, *Amphiasma merenskyanum* Brem., and *A. divaricatum* (Engl.) Brem. are distylous (Bremekamp, 1952). *Pentanisia variabilis* Haw. is reportedly distylous and *Tricalysia sonderiana* Hiern. is seemingly homostylous (Medley-Wood, 1902). I have seen no reports concerning distyly in South African representatives of *Spermacoce*, *Borreria*, *Anthospermum*, *Grumilea*, *Mussaenda*, or *Pentas*, genera for which distyly has been reported in species that occur elsewhere (Vuilleumier, 1967).

SANTALACEAE

Hill (1915) suggested the "possibility" that heterostyly may occur in *Thesium*, although the floral morphology of two species was "not quite convincing". Levyns (1940) stated that "it is clear that the phenomenon of heterostyly is not a feature of these plants". It is possible that interspecific differences in relative lengths of styles and stamens might have been responsible for Hill's supposition.

TURNERACEAE

Heterostyly is widespread in Turneraceae and is associated with a strong incompatibility system in the New World *Piriqueta caroliniana* (Walt.) Urb. (Ornduff & Perry, 1964) and *Turnera ulmifolia* L. (Lock, 1904; Martin, 1965). In South Africa, *Wormskioldia longipedunculata* Maxw. is distylous. Various features of its floral morphology have been documented and illustrated by Vogel (1955) although it is unknown whether this species has an incompatibility system. The closely related *W. pilosa* Schweinf. is homostylous (Urban, 1883) and, by analogy with homostylous species in other genera of the family, it is probably self-compatible. The description given of *Turnera oculata* Story suggests that it is homostylous (Story, 1961).

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